

# Performance across extreme environments: comparing waterfall climbing among amphidromous gobioid fishes from Caribbean and Pacific Islands

by

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**ABSTRACT.** - Amphidromous gobioid fishes have colonized streams on tropical and subtropical volcanic islands across the globe. Such streams are often characterized by steep gradients, high velocity currents, and even waterfalls as in-stream obstacles; however, the ability to climb waterfalls has evolved in many goby species, allowing juveniles returning from the ocean to penetrate upstream reaches. Past studies of Hawaiian gobioid fishes have identified two functionally different climbing techniques that were characterized by differing kinematics: a style described as 'powerbursting' among species with small juveniles (~1.5 cm body length), and a style described as 'inching-up' among species with large juveniles (~2.2 cm body length). These results suggested a potential size limit to the use of powerburst climbing, and indicated that functional diversity can exist even in extreme environments. In this study, we used standard- and high-speed video to assess kinematic and performance parameters of juvenile and adult *Sicydium punctatum* from the Caribbean island of Dominica, and compared the results with data previously obtained for two species of climbing gobioid fishes from the Hawaiian Island chain, *Sicyopterus stimpsoni* and *Lentipes concolor*. Although nearly as large as the 'inching' climber *S. stimpsoni*, climbing kinematics of juvenile *S. punctatum* were similar to those of powerbursting juvenile *L. concolor*. Nonetheless, adults of all three species converged on a climbing style similar to that of the inching-up climber *S. stimpsoni*, still suggesting a size limit for the powerburst climbing style of *L. concolor* and *S. punctatum*. Results of this study provide for a refined understanding of how functional diversity can be maintained in extreme environments across a broad geographic range and taxonomic diversity, and shed light on ontogenetic constraints in locomotor function.

**RÉSUMÉ.** - Performance en environnement extrême : comparaison de la capacité à franchir les cascades chez les gobies amphidromes des îles des Caraïbes et du Pacifique.

Les gobies amphidromes ont colonisé les rivières des îles volcaniques tropicales et subtropicales. Ces rivières sont souvent caractérisées par de fortes pentes, des courants rapides, et des cascades qui constituent des obstacles. La capacité de franchir ces cascades a évolué chez plusieurs espèces de gobies, et permet aux juvéniles qui arrivent de la mer de migrer en amont des rivières. Des études précédentes menées sur les gobioides d'Hawaï ont permis d'identifier deux techniques différentes pour franchir les obstacles, caractérisées par différentes cinématiques: une technique consiste à utiliser la poitrine pour pousser chez les espèces qui ont de petits juvéniles (~1,5 cm LT), et une technique utilisant la bouche et la ventouse chez les espèces qui ont de gros juvéniles (~2,2 cm LT). Ces résultats suggèrent une taille limite potentielle pour l'utilisation de la poitrine pour monter, et indiquent que de la diversité fonctionnelle peut exister même dans les environnements extrêmes. Dans cette étude, nous avons utilisé la vidéo standard et accélérée pour accéder aux paramètres de la performance et de la cinématique des juvéniles et adultes de *Sicydium punctatum* des îles de la Dominique, que nous avons comparé aux résultats obtenus précédemment sur les espèces hawaïennes *Sicyopterus stimpsoni* et *Lentipes concolor*. Bien que presque aussi grand que *S. stimpsoni*, la cinématique d'escalade des juvéniles de *S. punctatum* est semblable à celle des juvéniles de *L. concolor*. Néanmoins, les adultes des trois espèces convergent vers un style d'escalade semblable à celui du *S. stimpsoni* (utilisant la bouche et la ventouse), suggérant une taille limite pour la poussée par la poitrine de *L. concolor* et *S. punctatum*. Les résultats de notre étude permettent d'apporter des éléments de compréhension sur comment la diversité fonctionnelle peut être maintenue en environnement extrême, et ce à travers des aires géographiques très distantes et des espèces différentes.

Key words. - Amphidromy - Goby - Locomotion - Waterfall climbing - Kinematics - Sicydiinae.

Gobies are the most diverse lineage of teleosts, with over 2000 named species (Lauder and Liem, 1983; Thacker, 2003). In addition to a wide range of strictly marine taxa, several goby species with amphidromous life cycles have penetrated freshwater habitats of oceanic islands (McDowall, 2001, 2003, 2004). Larvae of amphidromous species hatch

upstream, and are then swept by currents to the ocean where they develop for several months before returning to adult stream habitats. Amphidromy places high demands on the anatomy, physiology and behaviour of teleosts, which have to adjust to radically different environments at least twice during their life cycle (Iida *et al.*, 2010; Valade *et al.*, 2009).

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While the physiological challenges of osmoregulation (e.g., Dutil *et al.*, 1987) and the behavioural challenges of radically different environments (e.g., McCleave and Wippelhauser, 1987) have been documented frequently in the literature, the locomotor challenges associated with migration between oceanic and fresh water habitats are often overlooked. However, these challenges may also present opportunities to study locomotor performance in boundary-environments and to assess the selective forces of extreme environments on locomotor performance. Among these locomotor challenges, waterfall climbing in gobioid fishes, which has evolved multiple times across tropical and subtropical oceanic islands (Keith, 2003; Thacker, 2003), presents a particularly opportune system to evaluate the constraints placed on amphidromous fishes by locomotor performance demands.

The waterfall-climbing gobioid fishes provide an excellent system for comparisons of locomotor performance across taxa due to their diversity and distinctive amphidromous life history that includes the migration of juveniles into freshwater stream habitats. To reach adult habitats on many steep, volcanic islands, juveniles must climb substantial waterfalls that are tens or hundreds of meters tall (Fitzsimons and Nishimoto, 1995; Nishimoto and Kuamo'o, 1997; Nishimoto and Fitzsimons, 1999) (Fig. 1). Waterfall-climbing may provide strong fitness advantages by providing a

means to reach breeding habitats and evade non-climbing predators (Schoenfuss and Blob, 2007; Blob *et al.*, 2010).

Previous studies have identified two climbing styles in waterfall-climbing Hawaiian gobies (Schoenfuss and Blob, 2003). "Powerburst" climbing, found in *Lentipes concolor* Gill, 1860, consists of a single, rapid cycle of pectoral fin adduction followed by short bursts of axially powered swimming against the falling water, interspersed with long rest periods during which the fish adheres to the waterfall with its pelvic suction disk. In contrast, the "inching-up" climbing style, only found in *Sicyopterus stimpsoni* Gill, 1860, allows the fish to remain attached to the surface of the waterfall using the alternate attachment of the pelvic suction disk and an oral sucker, allowing for steady progress upwards. The oral sucker develops concurrently with the second amphidromous migration of this species from the ocean back into fresh water. Upon arriving in stream estuaries, *S. stimpsoni* undergoes a dramatic cranial metamorphosis that results in the mouth moving ventrally and the upper lip enlarging dramatically (Schoenfuss *et al.*, 1997; Keith *et al.*, 2008; Iida *et al.*, 2010). Following this metamorphosis, the mouth, particularly the enlarged upper lip and the oral velum, becomes a secondary locomotor organ that is needed for the inching-up climbing style. Given the much larger size of incoming juvenile *S. stimpsoni* when compared with the

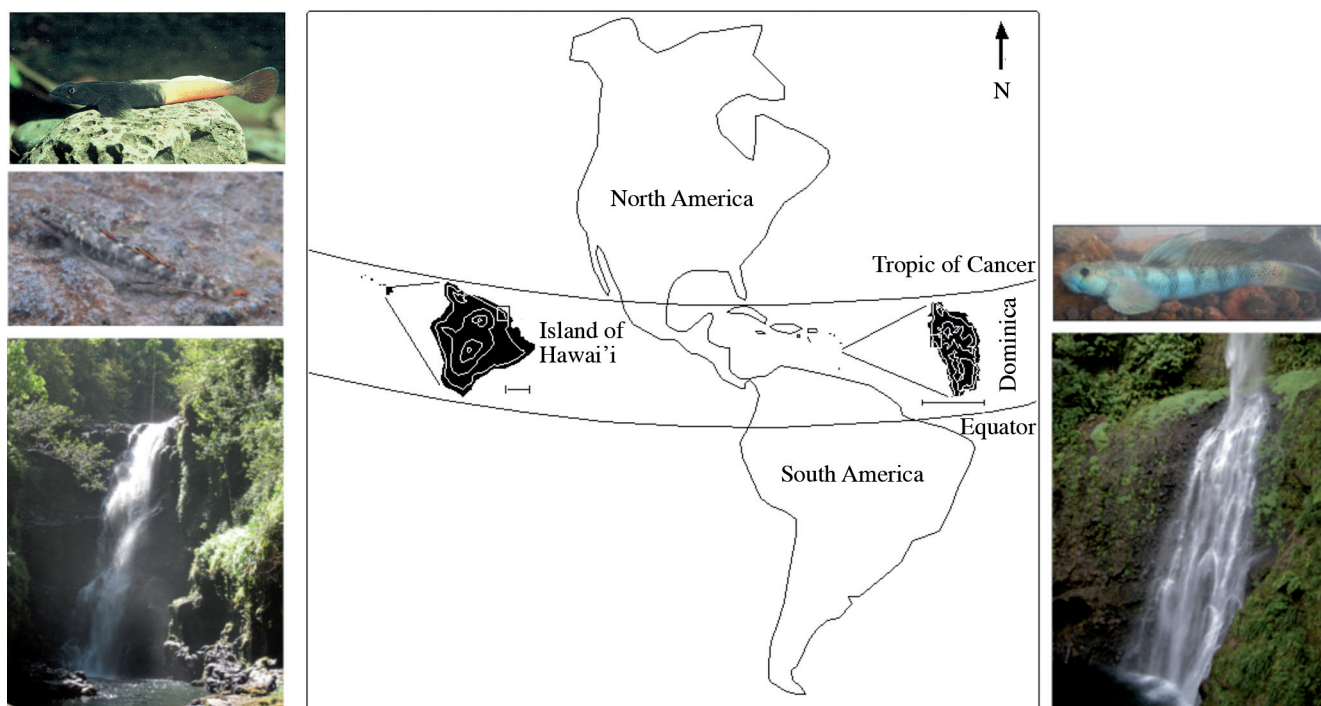


Figure 1. - Photographs of each species along with the location of field sites from which newly recruited juveniles and or adults were collected for climbing selection trials. Figure not to scale. Square box on each island indicates the location of Hakalau Stream on the Island of Hawai'i and Batali and Checkhall Rivers on Dominica. Scale bar by each island indicates 30 km. Top left = *Lentipes concolor* from the Island of Hawai'i; middle left = *Sicyopterus stimpsoni* from the Island of Hawai'i. Bottom left = waterfall on Hakalau Stream on the Island of Hawai'i. Top right = *Sicydium punctatum* from Dominica. Bottom right = Middleham Falls on Dominica, a waterfall approximately 100m tall that is too high for *S. punctatum* to climb.

powerburst climbing Hawaiian gobioid fish *L. concolor*, we have hypothesized previously that the powerburst climbing style may be limited to smaller individuals. This hypothesis was corroborated by the observation that the two species of gobioid fishes that utilize powerburst climbing during juvenile migrations converge on a climbing style more similar to that observed in inching-up climbing gobies as they grow to adult size (Blob *et al.*, 2007). The evaluation of climbing performance in Hawaiian gobioid fishes demonstrated diversity in locomotor styles and performance, which was surprising considering the extreme locomotor challenge of climbing waterfalls (Blob *et al.*, 2006).

Although diversity in climbing styles and locomotor performance was unexpected, both of these species of climbing Hawaiian gobioid fishes (*L. concolor*, *S. stimpsoni*) have very similar environmental conditions to cope with, including the need to climb waterfalls immediately upon entering freshwater habitats and the lack of predators once waterfalls have been climbed successfully. To evaluate how waterfall-climbing performance may be influenced by other environmental parameters, we conducted artificial waterfall-climbing trials on juveniles and adults from a species of climbing goby from a different ocean basin, *Sicydium punctatum* Perugia, 1896 from the Caribbean island of Dominica (Bell, 1994). We then compared our results to those reported in Schoenfuss and Blob (2003) and Blob *et al.* (2006, 2007) for *S. stimpsoni* and *L. concolor* from the Island of Hawai'i. Erosion in many Dominican streams has moved waterfalls further inland and allowed piscivorous predators (including climbing fish of the clingfish genus *Gobiesox*) to colonize upstream reaches, thus providing divergent environmental conditions for Dominican streams from those in which climbing has evolved in Hawaiian species. In addition, juveniles of *S. punctatum* are intermediate in size between juveniles of the smaller powerburst climber *L. concolor* and the larger inching-up climber *S. stimpsoni* (Schoenfuss and Blob, 2003), providing an opportunity to study size-related performance issues. *S. punctatum* does not possess the enlarged upper lip and velum used by *S. stimpsoni* in its inching-up climbing style, but *S. punctatum* juveniles might be too large to use powerburst climbing effectively. Because these three fish species independently invaded steep volcanic islands in separate ocean basins (Thacker, 2003), they provide an excellent opportunity to assess performance in the context of a similar locomotor challenge across ontogenetic, taxonomic and geographic scales. In this context, the goals of this study were (1) to evaluate the potential use of powerburst climbing mechanics in *S. punctatum* with its relatively large juveniles, and (2) compare the climbing performance of juvenile and adult *S. punctatum* with those of Hawaiian climbing goby species from the Pacific basin.

## MATERIALS AND METHODS

### Fish collection

Juveniles of Dominican *Sicydium punctatum* Perugia, 1896 were collected with dip nets from the lower reaches of the Batali River (near its mouth into the Caribbean Sea) in May 2008 (Fig. 1). Based on their translucent bodies, all fish were assumed to be recent recruits into fresh water (Schoenfuss *et al.*, 1997; Valade *et al.*, 2009). *Sicydium punctatum* can closely resemble the less common congener *Sicydium plumieri* (Bloch, 1786) (syn. *Sicydium antillarum* Ogilvie-Grant, 1884) (Brockmann, 1965; Bell, 1994). Following kinematic analysis, juvenile specimens were preserved and later examined under a dissecting scope for species confirmation (Brockmann, 1965).

Approximately 100 juveniles were collected downstream from, or while climbing, a low (1 m) bank of stones that formed the first small waterfall encountered during their migration upstream (approximately 30 m upstream from the ocean). Within 5 h of collection, specimens were transported in aerated containers to the Archbold Tropical Research and Education Center, in Springfield, Dominica, and a subset of approximately 50 juveniles were acclimated for several days prior to conducting climbing trials (survival was near 100%) (Tab. I).

Twenty-five adult *S. punctatum* were collected using 'opae nets' (bowl-shaped mesh nets with a narrow mouth) from the Check Hall River (Tab. I), located adjacent to the Archbold Tropical Research and Education Center, in Springfield, Dominica. The collection location for adult fish was at an altitude of approximately 450 m and approximately 4.5 km upstream of the river mouth. Collected fish were placed in aerated containers and acclimated overnight at ambient stream temperatures prior to conducting climbing trials. During collection, effort was made to use field marks described by Brockman (1965) to distinguish *S. punctatum* from its morphologically similar congener *S. plumieri*. Following climbing trials, specimens were preserved and examined under a dissecting scope to confirm species identification (Brockman, 1965).

### Waterfall climbing apparatus

Juvenile and adult *S. punctatum* were exposed to climbing trials that replicated the methods used by Schoenfuss and Blob (2003) and Blob *et al.* (2006, 2007) in analyses of locomotor performance of waterfall-climbing gobioid fishes (*S. stimpsoni* and *L. concolor*) from the Island of Hawai'i. Use of similar procedures for all three species permitted direct comparison of results.

Juvenile and adult *S. punctatum* were filmed climbing artificial surfaces using both 30Hz digital video recordings and 125Hz high-speed digital recordings. The experimental apparatus for the video recordings consisted of a chute with

Table I. - Mean values and standard deviations of morphological, kinematic, and performance variables for juveniles and adults of waterfall climbing stream gobies from Dominica (*Sicydium punctatum*) and Hawai'i (*Sicyopterus stimpsoni*, *Lentipes concolor*). Data for Hawaiian gobioid fishes are derived from previously published studies (Schoenfuss and Blob, 2003; Blob *et al.*, 2006, 2007). Superscript letters (a, b, c) indicate significant differences between treatments ( $p < 0.05$ , Kruskal-Wallis with Dunn's post test); number in parentheses indicates the sample size of locomotor events from which data were collected with each cycle from a different individual unless otherwise noted. Sample sizes differ between some values for the same species due to analysis limitations. BL/s indicates climbing velocity adjusted to relative size of each fish (Body lengths/second). <sup>1</sup> data derived from 30Hz DV recordings; <sup>2</sup> data derived from high-speed video recordings; <sup>3</sup> from 15 individuals; <sup>4</sup> from 12 individuals; <sup>5</sup> from 9 individuals; <sup>6</sup> from 25 individuals.

	Juvenile				Adult			
	<i>S. punctatum</i>	<i>S. stimpsoni</i>	<i>L. concolor</i>	<i>p</i> -value	<i>S. punctatum</i>	<i>S. stimpsoni</i>	<i>L. concolor</i>	<i>p</i> -value
Fish length <sup>1</sup> [cm]	1.9 <sup>a</sup> (40)	2.2 <sup>b</sup> (17)	1.4 <sup>c</sup> (17)	< 0.0001	6.3 ± 0.8 <sup>a</sup> (15)	5.4 ± 1.2 <sup>b</sup> (25)	6.1 ± 1.1 <sup>a</sup> (43)	0.0165
Fin excursion <sup>2</sup> [max angle]	108 ± 14.8 <sup>a</sup> (33) <sup>3</sup>	not applicable	124 ± 10.2 <sup>b</sup> (7)	< 0.0001	121 ± 16.7 <sup>a</sup> (50) <sup>6</sup>	39 ± 12.4 <sup>b</sup> (23)	107 ± 29.2 <sup>a</sup> (32)	< 0.0001
Cycle duration <sup>2</sup> [s]	0.25 ± 0.06 <sup>a</sup> (33) <sup>3</sup>	0.24 ± 0.05 <sup>a</sup> (26) <sup>4</sup>	0.02 ± 0.00 <sup>b</sup> (17) <sup>5</sup>	< 0.0001	0.17 ± 0.03 <sup>a</sup> (50) <sup>6</sup>	0.25 ± 0.03 <sup>b</sup> (23)	0.23 ± 0.05 <sup>b</sup> (32)	< 0.0001
Climbing bout duration <sup>1</sup> [s]	2.47 ± 1.8 <sup>a</sup> (40)	7.55 ± 6.5 <sup>b</sup> (17)	1.97 ± 0.7 <sup>a</sup> (17)	< 0.0001	2.74 ± 0.6 <sup>a,b</sup> (15)	4.72 ± 3.1 <sup>a</sup> (25)	2.74 ± 2.6 <sup>b</sup> (43)	0.0006
Climbing-only speed <sup>1</sup> [cm/s]	1.04 ± 0.50 <sup>a</sup> (40)	0.34 ± 0.07 <sup>b</sup> (17)	0.94 ± 0.14 <sup>a</sup> (17)	< 0.0001	0.69 ± 0.46 <sup>a</sup> (15)	0.99 ± 0.47 <sup>b</sup> (25)	1.15 ± 1.4 <sup>a,b</sup> (43)	0.0382
[BL/s] <sup>1</sup>	0.55 ± 0.26 <sup>a</sup> (40)	0.15 ± 0.03 <sup>b</sup> (26)	0.67 ± 0.10 <sup>a</sup> (17)	< 0.0001	0.12 ± 0.09 <sup>a</sup> (15)	0.17 ± 0.11 <sup>ab</sup> (25)	0.22 ± 0.20 <sup>b</sup> (43)	0.0095
Net climbing speed <sup>1</sup> [cm/s]	0.26 ± 0.34 (40)	0.22 ± 0.07 (17)	0.21 ± 0.09 (17)	= 0.74	0.23 ± 0.15 <sup>a</sup> (15)	0.71 ± 0.49 <sup>b</sup> (25)	0.99 ± 1.30 <sup>b</sup> (43)	< 0.0001
[BL/s] <sup>1</sup>	0.14 ± 0.18 (40)	0.10 ± 0.03 (17)	0.15 ± 0.06 (17)	< 0.048	0.04 ± 0.03 <sup>a</sup> (15)	0.13 ± 0.09 <sup>b</sup> (25)	0.07 ± 0.05 <sup>a</sup> (43)	< 0.0001
% time in motion <sup>1</sup>	22.4 ± 13 <sup>a</sup> (40)	54.3 ± 21 <sup>b</sup> (16)	22.3 ± 11 <sup>a</sup> (17)	< 0.0001	33.4 ± 10 <sup>a</sup> (15)	66.8 ± 16 <sup>b</sup> (25)	37.1 ± 19 <sup>a</sup> (43)	< 0.0001

water running over its surface. After acclimation, juvenile or adult *S. punctatum* were placed into a 60 x 45 x 15 cm basin (half-filled with stream water and containing a rock to provide cover), and challenged to climb the first 20 cm segment of the artificial waterfall chute. The chute was made from plastic rain gutter extending at an angle of 70° from the basin, in which fine-grained sand had been glued to the climbing surface. Stream water was washed over the chute prior to climbing trials to remove chemical residue. Flow over the climbing surface (200 ml/min, 1-1.5 mm depth) was generated by gravity feed from a siphon connected to a bucket of stream water.

#### Measurements of climbing kinematics and performance

Detailed methods for the recording and analysis of kinematics and performance for Hawaiian gobioid fishes are described in our previous studies (Schoenfuss and Blob, 2003; Blob *et al.*, 2006, 2007) and were matched closely for recordings of Dominican *S. punctatum*. Two types of video records were collected. First, to measure climbing performance over a distance of several body lengths, a Sony (Tokyo, Japan) DTV 1020 digital camcorder (30 Hz framing rate) filmed animals in dorsal view as they ascended the chute. Briefly, the camera was positioned to cover a field of view of approximately 20 cm of the chute at 10 cm above the water

level. Juveniles were placed into the basin below the chute in groups of five to seven individuals to accommodate their tendency to climb 'en masse' (Schoenfuss and Blob, 2003; Blob *et al.*, 2008, 2010). Body length was also calculated based on these recordings. Adults were placed into the basin in groups of 2-4 fish to stimulate climbing behaviour (Blob *et al.*, 2007). Each fish was used in a single trial and trials were only analysed if the fish climbed the entire 20 cm. DV tape footage (30Hz) was transferred to a computer (Macintosh G4) using iMovie software. Individual animals were tracked frame by frame. The beginning and end of each climbing bout were recorded, as were rest periods between bouts and instances of pectoral fin and tail use during climbing. Adult body length was measured with digital callipers to the nearest 0.1 cm.

Second, to evaluate detailed climbing kinematics, high-speed digital video was collected for a subset of trials using a Redlake Motionscope M1 (Cheshire, CT, USA) digital camera filming at 125Hz. Fish were filmed in dorsal view as they climbed the chute and trials were saved as AVI files. The positions of anatomical landmarks on the fishes were digitized for each analysed video frame using a modification of the public domain NIH Image program for Macintosh, developed at the US National Institutes of Health (the modification, QuickImage, was developed by J. Walker and



is available at <http://www.usm.maine.edu/~walker/software.html>). Points at the base and tip of both pectoral fins were digitized along with three points on the head representing the anterior midline of the face and the left and right eyes. At least nine additional points along the body midline were also digitized, with the most posterior point at the base of the caudal peduncle. Custom codes in MATLAB (Version 5.0; Mathworks, Inc.; Natick, MA, USA) were used to calculate kinematic variables from digitized coordinates. For all trials, fin movements and the displacement of the front lip through each cycle were evaluated. The angle of each fin to the direction of travel (determined by the two midline head points) was calculated for each frame, allowing us to calculate profiles of fin movements throughout locomotor cycles and maximum fin excursion angles. To calculate axial kinematics, 101 equally spaced points were interpolated for each frame from the points digitized along the dorsal midline, using QuicKurve software (Walker, 2000; program available at <http://www.usm.maine.edu/~walker/software.html>). From these interpolated points, we extracted the coordinates of 11 evenly spaced points along the length of the body to divide the body into 10 segments, each of which was 10% body length. Custom Matlab routines were used to calculate the following parameters for every frame of each locomotor cycle analysed: (1) the angle of each body segment to the direction of travel, (2) the amplitude of each landmark point relative to a straight body midline, and (3) the instantaneous resultant velocity of each landmark point. Measurements of segment angles and undulatory amplitudes along the body helped to identify which parts of the fish contribute to thrust generation: during undulation on terrestrial substrates, points along the body, where low minimum resultant velocities and low undulatory amplitudes coincide, indicate the primary regions where propulsive forces are generated (Gillis, 1998).

### Statistical analysis

Statistical analyses were performed using GraphPad Prism 5.0 (San Diego, CA, USA) or Statview 5.0 (SAS Institute Inc, Cary, NC, USA) for Macintosh. The mean locomotor cycle duration and maximum fin angle for each species were calculated from high-speed video, whereas the mean durations of climbing bouts, climbing velocities, and the percent time spent in motion for entire climbing bouts (over the 20 cm distance) were calculated from standard video. Net climbing speed (accounting for rest periods) was calculated by dividing the 20 cm distance by the sum of climbing and rest times. 'Climbing-only' climbing speed, based only on the time during which the fish was actively climbing, was also calculated from standard video. In addition, the percentage of time that each individual spent moving was calculated as time in motion divided by the sum of motion and rest times. Differences in kinematic and performance variables across all three species were evaluated using nonparametric

Kruskal-Wallis analysis with a Dunn's post-test. A Mann-Whitney *U*-test was used to evaluate differences between conspecific juveniles and adults.

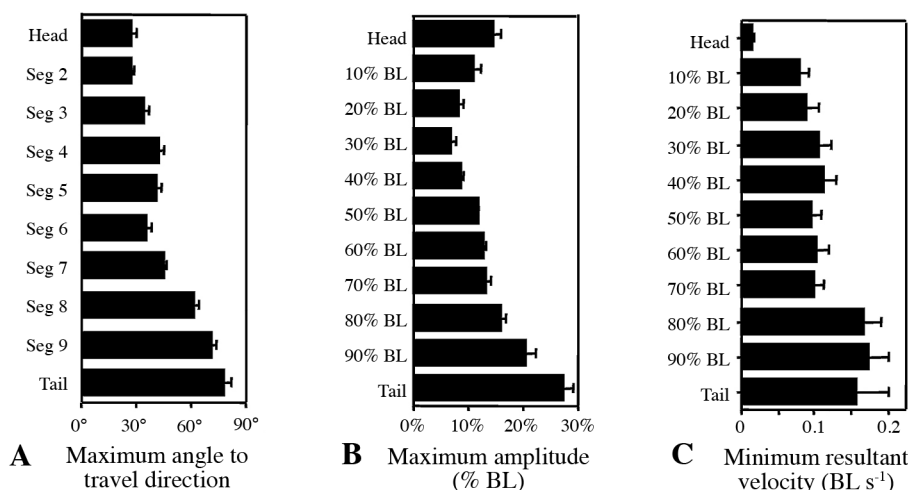
## RESULTS

### Juvenile climbing kinematics and performance

Among the species, the Dominican goby *Sicydium punctatum* was intermediate in size between the significantly smaller Hawaiian powerburst climber *L. concolor* and the Hawaiian inching-up climber *Sicyopterus stimpsoni* (Tab. I). Like the Hawaiian species, juvenile *S. punctatum* readily climbed the artificial waterfalls provided as a climbing surface, using kinematics that strongly resembled those of the powerburst climber *Lentipes concolor*. Climbing bouts for juvenile *S. punctatum* began with a single phase of adduction of the pectoral fins, followed by axial undulations. Phase lag between adduction of the left and right fins was minimal in both *S. punctatum* (mean  $\pm$  S.E. =  $27 \pm 4\%$  cycle duration) and *L. concolor* ( $10 \pm 2\%$  cycle duration: Schoenfuss and Blob, 2003), and did not differ significantly between the species. However, a Mann-Whitney *U*-test indicated a smaller maximum fin angle at the onset of the locomotor cycle in *S. punctatum* when compared with *L. concolor* (Tab. I: juvenile *S. stimpsoni* do not frequently use pectoral fins or body axis undulations during waterfall climbing (Schoenfuss and Blob, 2003) and were excluded from these comparisons). Furthermore, the speed of fin adduction in juvenile *S. punctatum* (mean  $\pm$  S.E.  $2.4 \pm 0.2$  ms<sup>-1</sup>) was significantly slower, only half that observed in juvenile *L. concolor* ( $6.3 \pm 0.9$  ms<sup>-1</sup>: Schoenfuss and Blob, 2003) ( $p < 0.0001$ , Mann-Whitney *U*).

Movements of the body axis by *S. punctatum* produced large maximum angles of all body segments relative to the direction of travel (mean maximum =  $27^\circ$ - $77^\circ$  per segment,  $N = 22$  cycles; Fig. 2A), particularly toward the tail. Anteriorly these angles were similar in magnitude to those shown by *L. concolor* ( $\sim 30^\circ$ ), but posteriorly *L. concolor* showed larger values ( $\sim 60^\circ$ : Schoenfuss and Blob, 2003). Peak amplitudes were also high along the entire length of the body (Fig. 2B), ranging from approximately 7% body length at point 4 (located at 30% body length from the head), to much higher values (27% body length) at the tail that exceed those shown by *L. concolor* ( $\sim 20\%$ : Schoenfuss and Blob, 2003). The lowest lateral displacements occurred at points closest to the pelvic sucker, approximately 20-40% posteriorly along the length of the body (points 3, 4 and 5: Fig. 2B). Minimum resultant velocities of points along the body were lowest at the head but, like maximum angles and amplitudes, greatest at the tail (Fig. 2C), though all magnitudes ( $< 1$  BL s<sup>-1</sup>) were lower than those shown by *L. concolor* ( $> 8$  BL s<sup>-1</sup>: Schoenfuss and Blob, 2003).

Figure 2. - Axial kinematics during vertical powerburst climbing by juvenile *Sicydium punctatum*. **A**: Maximum angles of body segments to the direction of travel. Bars for each equal-length segment plot the mean ( $\pm 1$  S.E.,  $N = 22$  cycles) maximum angle of the segment to the direction of travel at any point during the cycle. **B**: Mean ( $\pm 1$  S.E.,  $N = 22$  cycles) maximum amplitudes throughout the climbing cycle for each of 11 equally spaced points along the length of the fish, normalized as a percentage of body length. **C**: Mean ( $\pm 1$  S.E.,  $N = 22$  cycles) minimum resultant velocities throughout the climbing cycle for the same 11 equally spaced points along the length of the fish, in  $\text{BL s}^{-1}$ .



Despite similarities in climbing kinematics between *S. punctatum* and *L. concolor*, duration of the climbing cycle (approximately one quarter of a second) for *S. punctatum* matched durations previously recorded for the inching climber *S. stimpsoni*, which were significantly slower than values for *L. concolor* (20 ms: Tab. I; Schoenfuss and Blob, 2003). However, the duration of entire climbing bouts was relatively brief for both *S. punctatum* and *L. concolor* and only one third of the climbing bout duration observed in *S. stimpsoni*. The climbing-only speed (excluding rest periods) normalized to body length was again closely matched for *S. punctatum* and *L. concolor*, with *S. stimpsoni* considerably slower (Tab. I). However, considering the greater amount of time spent resting by *S. punctatum*, its net climbing speed (adjusted for body size) was similar to that of *S. stimpsoni*. Revised calculations of data from our earlier studies (Blob *et al.*, 2006) indicate that *L. concolor*, which had a similar % time in motion as *S. punctatum* (Tab. I), also was comparable in net climbing performance with the other two species.

### Adult climbing performance

Similar to juveniles, adults of all three species readily climbed the artificial waterfalls. While juvenile sizes differed by as much as 50% between species, body lengths of adult fishes used in our experimental trials differed by less than 10%, with the specimens of *S. punctatum* in our experiments slightly larger than those of the other two species previously analysed. Climbing kinematics for *S. punctatum* adults resembled those of *L. concolor* adults (Blob *et al.*, 2007), with cycles of pectoral fin adduction accompanying each cycle of upward advancement, not just the initial phase of the climbing bout.

Front lip displacement and fin movement are tightly coupled with the front lip not exhibiting upward displacement until the pectoral fins begin their adduction move-

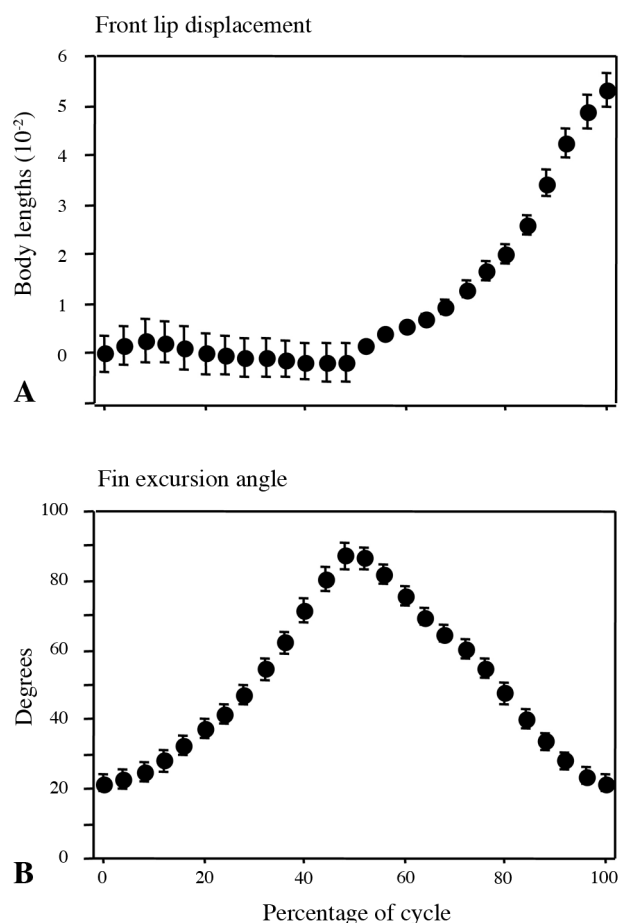


Figure 3. - Mean profiles of kinematic variables in *Sicydium punctatum* adults ( $N = 50$  cycles). **A**: Cumulative displacement of the front lip from the start of the climbing cycle. **B**: Excursion angle of the pectoral fin. Each climbing cycle was normalized to the same duration and values of kinematic variables were interpolated for 101 equally spaced increments through the cycle using QuickSAND software (Walker, 1998). Plots for each variable illustrate means  $\pm 1$  SE for each 4% increment of time through the cycle.

ment at approximately the half-way point of the climbing cycle (Fig. 3). Interestingly, the front lip displacement in *S. punctatum* is smaller as a proportion of body length than was observed in *L. concolor*, and more closely matches the front lip displacement of the inching-up climber *S. stimpsoni* (Blob *et al.*, 2007). In contrast, fin excursion angles for *S. punctatum* (Tab. I; Fig. 3) were similar to those of *L. concolor*, and significantly different from the much smaller fin excursion angles previously reported for *S. stimpsoni* (Blob *et al.*, 2007).

Climbing cycle duration was significantly shorter for *S. punctatum* when compared with the other two species, while the climbing bout duration for *S. punctatum* matched closely to that of *L. concolor* and was significantly shorter for both of these species compared to that of *S. stimpsoni* (Tab. I). The climbing-only speed attained by *S. punctatum* adults was slower than observed in both Hawaiian gobies, although the differences only achieved statistical significance in comparison with *L. concolor* (Tab. I). Interestingly, when rest periods were factored into climbing performance (normalized for body length), adult *S. punctatum* and *L. concolor* were more similar in net climbing speed and were both outperformed by adult *S. stimpsoni* (Tab. I).

#### Comparison of juvenile and adult waterfall climbing performance

Adult climbing gobies were several times the length and mass of their juveniles and, as a result, were expected to exhibit differences in climbing performance. Pectoral fin use, as described by the maximum fin excursion angle, increased slightly between juveniles and adults of *S. punctatum* ( $p = 0.0007$ , Kruskal-Wallis) and decreased for *L. concolor*, although standard deviations indicate quite variable values for this species. As described previously (Blob *et al.*, 2007), adult *S. stimpsoni* also use their pectoral fins to initiate climbing bouts. Surprisingly, given the larger size of the adults, cycle duration became shorter for adult *S. punctatum* compared to juveniles ( $p < 0.0001$ , Kruskal-Wallis). The duration of climbing bouts changed little for *S. punctatum* ( $p = 0.041$ , Kruskal-Wallis), while it shortened considerably for *S. stimpsoni* and increased for *L. concolor*. Similarly, climbing velocities did not exhibit parallel trends for the three species. When normalized for body length, climbing-only speed declined by three quarters for *S. punctatum* (Tab. I) and by a similar proportion for *L. concolor* between juveniles and adults. In contrast, for *S. stimpsoni*, adults retained almost exactly the same climbing-only speed relative to their body size when compared to their conspecific juveniles (Blob *et al.*, 2007). Factoring in rest periods, net climbing speeds declined for *S. punctatum* ( $p < 0.0001$ , Kruskal-Wallis) and *L. concolor*, the two powerburst climbing species, but increased slightly for *S. stimpsoni*. Finally, adults of all three species spent approximately 30% more

time in motion while climbing a 20 cm segment of the artificial waterfall than did their conspecific juveniles (*S. punctatum*:  $p = 0.004$ , Kruskal-Wallis).

## DISCUSSION

We compared waterfall climbing in juveniles and adults of the amphidromous climbing goby *Sicydium punctatum* from the Caribbean island of Dominica with similar data previously obtained from two Hawaiian species, *Sicyopterus stimpsoni* and *Lentipes concolor*. These comparisons allowed us to evaluate differences in climbing kinematics and performance across taxonomic, geographic, and ontogenetic scales. Additionally, the present study allowed us to evaluate the potential use of powerburst climbing mechanics in *S. punctatum* with its relatively large juveniles and examine whether this climbing style is constrained by body size.

Despite their larger size, juvenile *S. punctatum* exhibited a climbing style that was similar in fin use, lateral undulation of the body axis, length of locomotor bouts, and time in motion to that of juveniles from the Hawaiian powerburst climber *L. concolor*. These similarities included coincidence of the locations along the body axis of low undulatory amplitudes and resultant velocities near the location of the pelvic sucker (Fig. 2). However, with a body size close to that of inching-up climbers like juvenile *S. stimpsoni*, juvenile *S. punctatum* migrating into streams might have adopted additional kinematic mechanisms to aid climbing, such as the use of pectoral fin adduction with every locomotor cycle as seen in adult gobies (Blob *et al.*, 2007). Such kinematic adjustments were not evident among juvenile *S. punctatum* and, in fact, their larger size may be a factor contributing to their slower size-normalized climbing speed relative to the smaller powerburst climber *L. concolor* (Tab. I). Ascending approximately vertical surfaces entails high requirements for muscular power, but muscles contracting at high frequencies (such as in powerburst climbing) tend to have reduced power-producing capacities (Rome, 1998), and mass-specific power production tends to decrease with body size (Irschick *et al.*, 2003), potentially requiring larger powerburst climbers like *S. punctatum* juveniles to climb more slowly if they retain powerburst kinematics.

Similar to observations of *L. concolor* (Blob *et al.*, 2007), as *S. punctatum* grow larger their powerburst climbing style begins to resemble that of the inching-up climbing style of *S. stimpsoni*, although the lack of an oral sucker prevents true inching. Instead, *S. punctatum* and *L. concolor* rely on the bracing and propulsion achieved by protracting their pectoral fins beyond 90 degrees to the body axis, as indicated by their the large fin excursion angles (when compared with adult *S. stimpsoni*). Although adult *S. stimpsoni* also utilize their pectoral fins for bracing and possibly propulsion

near the onset of climbing bouts and/or climbing cycles, fin excursion angles never achieve the magnitude observed in *S. punctatum* and *L. concolor*. Further evidence of convergence in climbing styles across species as gobies grow in size is the reduced use of lateral undulation in *L. concolor* and *S. punctatum* when compared with their conspecific juveniles, producing patterns similar to inching in *S. stimpsoni*. The convergence of climbing styles among adults of all three species of waterfall climbing gobioids compared in this study further implicates the constraints exerted on climbing style by body size, with powerburst climbing not sustainable for larger fish. Elaborating on this issue that emerged in comparisons of juveniles of different sizes, power needs for climbing increase in larger fish because (i) power equals work divided by time, (ii) work equals force multiplied by the distance travelled, and (iii) the force required to move a climbing fish would increase with its body weight as it grows (Wilson *et al.*, 2000; Irschick *et al.*, 2003; Maie *et al.*, 2007).

Taxonomic relatedness was not a good predictor of climbing kinematics or climbing performance among the species we compared, as the more closely related *S. punctatum* and *S. stimpsoni* (Thacker, 2003; Keith *et al.*, 2010) exhibited more divergent climbing styles than *S. punctatum* and *L. concolor*. The lack of congruence between taxonomic relatedness and climbing style suggests that waterfall climbing may have evolved multiple times independently in gobioid fishes on oceanic islands, with all gobioids using their pelvic suction disks as a component in achieving waterfall climbing ability while supplementing other structures to either gain (i.e., sucker mouth in *S. stimpsoni*) or maintain (i.e., fin usage in *S. punctatum* and *L. concolor*) climbing ability.

Moreover, the fact that the two Hawaiian waterfall-climbing species achieved higher climbing velocities than *S. punctatum* (particularly as adults) suggests that other selective pressures on this species may interfere with enhancement of its climbing performance. Previous studies (Blob *et al.*, 2010) measured a morphological trade-off between body shapes that maximize waterfall climbing performance and predator avoidance performance for populations of *S. stimpsoni* exposed or sheltered from predators. In the Hawaiian Islands, the amphidromous habits of *S. stimpsoni* cause most individuals to have only a fairly brief exposure to predators as juveniles, because adults are found in stream segments above the extent of the non-climbing piscivore *Eleotris sandwicensis* Vaillant and Sauvage, 1875. In contrast, Dominican *S. punctatum* cohabit upstream reaches with the piscivorous clingfish *Gobiesox nudus* Linnaeus, 1758. It is possible that reduced climbing performance in *S. punctatum* is partially due to the need of this species to maintain body shapes optimised to avoid predation (Domenici *et al.*, 2008), rather than waterfall climbing ability, throughout their lifespan.

Taken together, our data from *S. punctatum* demonstrate that waterfall climbing ability has evolved multiple times in gobioid fishes, that climbing styles are constrained by body size, and that other locomotor needs such as predator avoidance may constrain optimization of climbing morphology and performance.

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